

# Revision of the Recent *Bullata* Jousseaume, 1875 (Gastropoda: Marginellidae) with the description of two new species

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## ABSTRACT

The genus *Bullata* Jousseaume, 1875 is revised based on conchological characters. All known living species are endemic to Brazil. Two new species are herein described, *B. guerrinii* and *B. analuciae*. *Bullata guerrinii* is most similar to *B. largillieri* (Kiener, 1841) as both have an enlarged second columellar plication which overrides and fuses with the first, but differs in having a darker coloration, wider aperture, and spire only slightly apparent. *Bullata analuciae* has similar color pattern to *B. largillieri*, but differs in having clearly separate first and second columellar plications, a generally larger, thinner shell, a broad aperture and non-denticulated lip. The other 4 known species are described and discussed and a key for identification is presented. A cladistic analysis of *Bullata* was made using 22 conchological characters (53 states). The single most parsimonious tree obtained (length 37, CI = 51, RI = 69) is as follows: (*B. bullata* (*B. analuciae* ((*B. largillieri*, *B. guerrinii*) (*B. lilacina*, *B. mattheusi*))). The monophyly of the genus is supported by 8 synapomorphies.

*Additional key words:* Volutoidea, Neogastropoda, new species, Brazil, phylogeny.

## INTRODUCTION

The genus *Bullata* Jousseaume, 1875 includes species that live in tropical waters from the intertidal down to 70 m. Recent species of the genus, as it is currently defined (Coovert and Coovert, 1995), are endemic to the continental shelf off Brazil. Yet, its fossil record can be traced to the Miocene of Trinidad (Maury, 1925) and the Mio-Pliocene of the southeastern United States (Redfield, 1870; Olsson, 1916).

As with most Marginellidae, throughout its taxonomic history, species of *Bullata* were earlier referred to the genus *Marginella* Lamarck, 1799. The genus was first

differentiated as a group by Swainson (1833) who erected the genus *Volutella*, a name preoccupied, however, by *Volutella* Perry, 1810 (= *Vasum* Röding, 1795). This designation was, nonetheless, widely used. In 1875, Jousseaume established *Bullata* as a replacement name for *Volutella* but put too much emphasis on the involute spire as a diagnostic character for included species. Thus, in Jousseaume's monograph, the genus was used to encompass species that later were assigned to other genera and families, such as *Closia* Gray, 1857, *Prunum* Herrmannsen, 1851, *Cryptospira* Hinds, 1844, *Granulina* Jousseaume, 1888; *Gibberula* Swainson, 1840; *Persicula* Schumacher, 1817 (the last 3 genera belong in the Cystiscidae). Coovert and Coovert (1995), in their recent taxonomic revision of the Marginellidae and Cystiscidae, provided a more refined diagnosis of the genus.

Similarly to what probably occurs with other marginellids, the two new species described herein have eluded Brazilian malacologists for a long time due to their limited ranges and subtly different conchological characters. Both species could easily be mistaken for *Bullata largillieri* (Kiener, 1841) due to somewhat similar color patterns.

This work is part of an ongoing revision of the Brazilian Marginellidae by the senior author. Institutional abbreviations used are: ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia; BMNH: The Natural History, London; BMSM: The Bailey-Matthews Shell Museum, Sanibel, Florida; GAC: collection of Gary A. Coovert; IBUFRJ: Instituto de Biologia/Universidade Federal do Rio de Janeiro, Rio de Janeiro; MNHN: Muséum National d'Histoire Naturelle, Paris; MNRJ: Museu Nacional/Universidade Federal do Rio de Janeiro; MORC: Museu Oceanográfico "Prof. Eliézer de Carvalho Rios", Rio Grande; MZUSP: Museu de Zoologia/Universidade de São Paulo, São Paulo; PMC: collection of Paulo Márcio S. Costa, Rio de Janeiro; USNM: National Museum of Natural History, Smithsonian Institution, Washington.

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## SYSTEMATICS

Family Marginellidae Fleming, 1828

Subfamily Marginellinae Fleming, 1828

Tribe Prunini Coovert and Coovert, 1995

Genus *Bullata* Jousseau, 1875

*Bullata* Jousseau, 1875: 167, 250, *nomen novum* for *Volutella* Swainson, 1833 (*non Volutella* Perry, 1810)

*Marginella* (*Volutella*) Swainson, 1833: (2)1, *Marginella* pl. 1 [type species: *Marginella bullata* Lamarck, 1822 = *Voluta bullata* Born, 1778; original designation] (*non Volutella* Perry, 1810)

*Gibberulina* Monterosato, 1884:139 (see Coovert, 1987: 27, for further details).

**Type species:** *Voluta bullata* Born, 1778; by tautonymy.

**Diagnosis:** Shell moderately large to very large for family; colored with bands or other patterns, narrowly to broadly obovate; spire immersed or nearly so; lip thickened, denticulation usually present, absent in some; posterior end of lip arched above apex; external varix present; varix groove adjacent to body whorl, distinctly colored; siphonal notch absent; parietal callus present to nearly obsolete in type species; columella with 4 strong plications occupying less than half the aperture but not crowded in anterior direction.

**Description:** Shell 14–98 mm in length, narrowly to broadly obovate (length: width ratio 1.53–1.83); surface glossy, unsculptured, with 4–5 whorls. Color pattern composed of indistinct darker spiral bands, with or without rows of irregular white spots. Spire immersed to very low and apparent, often covered by callus. Protoconch apparent to completely concealed. Outer lip moderately to heavily thickened, internally denticulated or smooth, with a distinct, colored external varix, particularly strongly colored in varix groove adjacent to the body whorl. Lip with or without a distinct, flattened, beveled area in anterior direction. Aperture narrow to moderately broad, wider in anterior direction, some species with an obscure to distinct trough or siphonal “gutter” (best seen in apical view). Parietal callus nearly obsolete to strongly developed; posterior callus nearly obsolete to strongly developed; left antero-ventral callus extending from the anterior end of varix to level of third plication, often resembling a fasciole. Columella straight to concave, with 4 strong plications; plications subequal, or the first and/or second strongly developed, sometimes fused; third and fourth plications confined to aperture or slightly emerging, distal ends truncate or gradually diminishing. Space between plications increases in posterior direction, fourth plication often remote. Plication angle increasing in posterior direction relative to longitudinal axis.

**Remarks:** Several authors (see species synonymy lists, *q.v.*) have variously combined *Bullata* and *Closia* Gray, 1857, apparently based on the superficial resemblance of shell shape, especially that of *B. lilacina* (Sowerby,

1846). *Closia* differs in a number of conchological characters, chiefly the very thin, very sharply formed plications that are strongly crowded in anterior direction. *Bullata*, on the other hand, has much thicker, rounded plications that are not nearly as crowded in anterior direction. The labial denticulation of *Closia* is sharply, regularly formed and widely spaced (i.e., separated by a distance greater than the thickness of a denticle). The labial denticulation in *Bullata* is irregularly formed and crowded or nearly absent. The columella in *Closia* is concave, resulting in a sinuous outline, while in *Bullata* the columella is more straight. *Closia* has a much more completely immersed spire and a tendency toward a much lighter shell. *Closia* is probably closely allied to *Ovaginella* (Coovert and Coovert, 1995: 87) and thus in the Austroginellini. *Bullata* has an oesophageal caecum just posterior to the nerve ring, type 6 radula (Coovert and Coovert, 1995: 56–57), and lacks the Valve of Leiblen, character states that allocate the genus placing it in the tribe Prunini. Also, these genera are restricted in their biogeography to specific oceanographic basins: *Bullata* to Southern West Atlantic and *Closia* to the Indian Ocean (Coovert and Coovert, 1995: 87). Thus, we consider *Closia* to be a separate and unrelated genus, which includes *C. sarda* (Kiener, 1834) as the type species, as well as *C. majuscula* (Martens, 1880) and *C. princeps* (Sowerby, 1901).

*Cryptospira angustata* (Sowerby, 1846) was included in *Bullata* by Jousseau (1875: 251), due to the immersed spire. But most species of *Cryptospira* can be differentiated by their much stronger fasciole-like callus, much stronger and more numerous columellar plications that occupy more than half the aperture, and extensive callusing posterior to varix. Thus we consider *Cryptospira* to be a separate genus with a separate origin but within the Prunini, with distribution restricted to the Indo-Pacific Region (Coovert and Coovert, 1995: 93).

Although described as *Bullata lipci* Clover, 1990, we agree with Lipe and Sunderland (1991:15), and consider this a species of *Prunum*, probably a close relative of *Prunum rostratum* (Redfield, 1870). The narrow shape of the shells, the ventral area of the body whorl just posterior to the plications, which is built up by callus and forms a groove just posterior to the first plication, and the very reduced, remote fourth plication, are very similar in these two species. Also both species are from the Yucatan region of Mexico. The involute shell of *Prunum lipci* (Clover, 1990) with the posterior end of the lip arching above the spire, represents a combination of shell traits that appears in other marginellid genera and, although present in *Bullata*, is not a diagnostic character this genus.

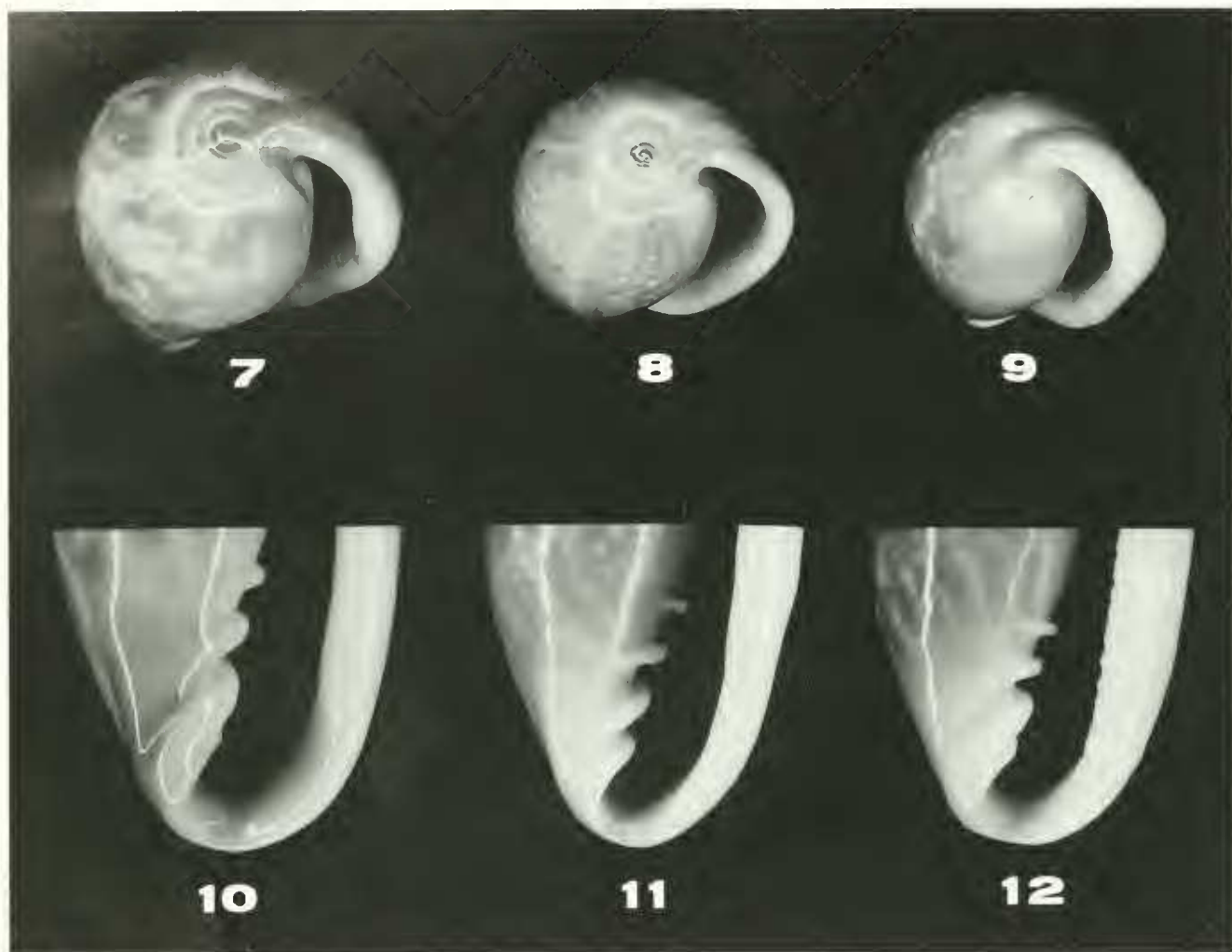
*Bullata guerrinii* new species  
(Figures 1, 7, 10)

**Diagnosis:** Color pattern of irregular, squarish cream spots; spire slightly but distinctly apparent, extremely



**Figures 1-6.** *Bullata* species in ventral and dorsal views. **1.** Holotype of *Bullata guerrinii* new species, MNRJ 7815, length 27.0 mm, width 16.5 mm. **2.** Holotype of *Bullata analuciae* new species, MNRJ 7156, length 27.0 mm, width 15.1 mm. **3.** *Bullata bullata* (Born, 1778), IBUFRJ 5471, length 52.1 mm, width 45.2 mm. **4.** *Bullata largillieri* (Kiener, 1841), PMC 939, length 21.3 mm, width 13.4 mm. **5.** *Bullata lilacina* (Sowerby, 1846), PMC 476, length 24.5 mm, width 14.9 mm. **6.** *Bullata mattheusi* van Mol and Tursch, 1967), PMC 937, length 39.0 mm, width 22.9 mm.



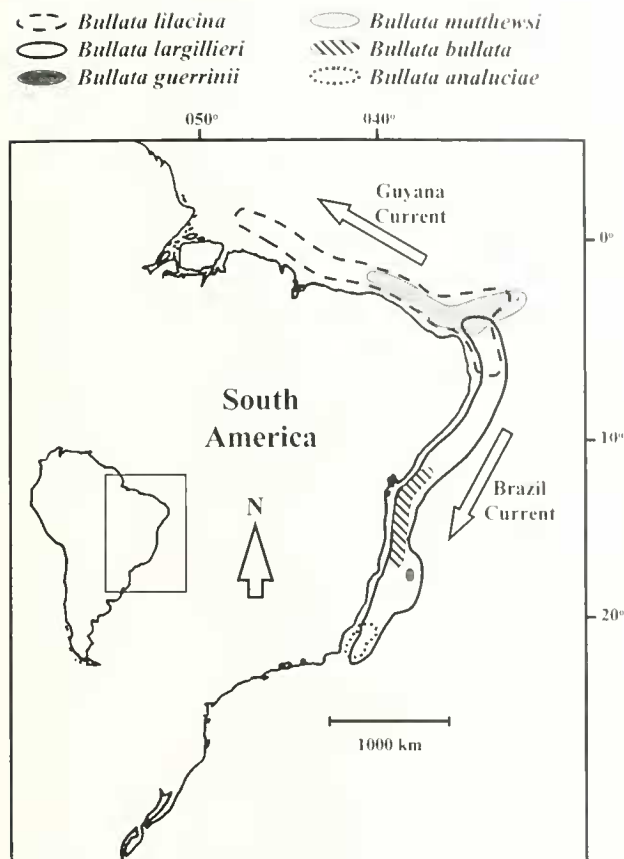


Figures 7–12. *Bullata* species: spire, posterior labial insertion, and columellar structures. 7, 10. Holotype of *Bullata guerrini* new species. 8, 11. Holotype of *B. analucia* new species. 9, 12. *B. largillieri* (Kiener, 1841), PMC 939.

low, dome-like, partially covered by posterior labial insertion and posterior parietal callus; aperture brown internally, becoming paler toward the lip; first and second plications distally fused, forming 1 strong plication ridge.

**Description:** Shell of medium size (25–29 mm in length), moderately heavy, obovate (length: width ratio 1.61–1.67,  $\bar{x} = 1.639$ ,  $s = 0.0199$ ,  $n = 6$ ), with approximately 4.5 whorls. Color pattern of irregular squarish cream spots, arranged in irregular axial rows, on purplish-brown background, crossed by 4 indistinct darker spiral bands (1 near suture, 2 narrower ones at mid-section of body whorl, 1 near anterior end). Spire extremely low, dome-like, slightly but distinctly apparent, partially covered by posterior labial insertion and posterior parietal callus. Protoconch visible or partially so, dark-brown. Outer lip thickened internally, with distinct, heavy external varix, thinning abruptly in posterior direction, with indistinct, flattened, beveled area thinning evenly in anterior direction, labial denticulation very fine, obsolete to indistinct, varix groove excavated. Outer

lip brownish-white, darkening toward varix groove. Aperture narrow, slightly wider than lip thickness when measured ventrally, wider in anterior direction and somewhat angled at posterior end. Aperture brown internally, becoming paler toward lip. Parietal wall convex with continuous ventral callus, thickening toward aperture, thinning abruptly along collabral line just outside aperture. Ventral callus extending in anterior direction, thinning but smoothly joining left antero-ventral callus. Posterior callus forming rounded mound separated from posterior lip insertion by notch. Left antero-ventral callus extending from anterior end of varix to level of fourth plication, with distinct furrow between second and third plications, and continuing as sharp, distinct, straight continuation of varix. Ventral callus whitish brown. Columella slightly concave, plications somewhat strong. First plication much weaker than second, both distally fused, forming 1 very strong plication ridge, separated from the parietal callus by distinct groove. Third plication stronger than fourth, weaker than plication ridge, extending



**Figure 13.** Geographic ranges of the living species of *Bullata*.

slightly outside aperture; fourth plication confined to aperture. Space between plications increasing in posterior direction, with fourth plication somewhat remote (i.e., distance between third and fourth plications distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally.

**Type material:** Holotype, MNRJ 7818 (length 27.0 mm, width 16.5 mm); Paratypes: BM(N11) 1996417 (length 23.3 mm, width 14.2 mm); IBUFRJ 10000 (length 25.7 mm, width 15.4 mm); MNHN (length 29.8 mm, width 18.3 mm); MZUSP 28849 (length 26.1 mm, width 15.7 mm); USNM 890896 (length 24.4 mm, width 15.1 mm), all from 40 km NE off Alcobaca, Bahia State, Brazil, 10–35 m.

**Type locality:** Pedra da Lixa (17°41.5' S, 038°59' W), Parcel das Paredes, 27 km E off Caravelas, Bahia State, Brazil, 5–15 m.

**Geographic range:** Known from type locality, and, according to local fishermen, from reefs around Abrolhos Archipelago (figure 13).

**Remarks:** *Bullata guerrinii* is most similar to *Bullata largillieri* (Kiener, 1841) in their color patterns and fused first and second plications (figures 10, 12). But these species differ in their shell shape, general color, spire

(figures 7, 9), ventral callusing, aperture width, shape of external lip, and shape of the third and fourth plications (figures 10, 12).

*Bullata guerrinii* is easily distinguishable from *B. bullata*, *B. lilacina* (Sowerby, 1846) and *B. matthewsi* (van Mol and Tursch, 1967), by its spotted color pattern, while the others have banded color patterns (figures 1–6).

For a summary of these differences, refer to dichotomous key included later in this paper.

**Etymology:** *guerrinii*: species dedicated to Mr. Ricardo Guerrini.

*Bullata analuciae* new species  
(Figures 2, 5, 11)

*Marginella (Closia) largillieri*.—Eisenberg, 1951: 126, fig. 5 (non Kiener, 1841).

*Marginella largillieri*.—Abbott and Dance, 1956: 234, unnumbered fig. (non Kiener, 1841).

*Bullata* aff. *bullata*.—Leal, 1990: 244.

*Bullata* cf. *largillieri*.—Lipe, 1991: 2–3, pl. 1, fig. 2.

*Bullata* sp.1.—Leal and Bouchet, 1991: 23.

*Closia* cf. *largillieri*.—Bozzetti, 1996: 54, unnumbered fig.

**Diagnosis:** Color pattern of small irregular cream spots arranged in axial rows, evenly superimposed on caramel-brown background, crossed by 4 indistinct darker spiral bands; labial denticulation absent or reduced to very obscure undulations; aperture wide, broader than lip thickness when measured ventrally; first and second columellar plications completely separate, subequal in size. Third plication is subequal in size to first 2, fourth plication weaker and confined to aperture.

**Description:** Shell small to medium (15–38 mm in length), obovate (length:width ratio 1.49–1.70,  $x = 1.618$ ,  $s = 0.0669$ ,  $n = 18$ ), with approximately 4 whorls. Surface glossy, without sculpture; color pattern of small, irregular cream spots arranged in axial rows, evenly superimposed on caramel brown background, crossed by 4 indistinct darker spiral bands (1 near suture, 2 narrower ones at mid-section of body whorl and 1 near anterior end). Spire almost completely immersed, flattened to slightly depressed, exposed but covered by glassy transparent callus, partially covered by posterior lip insertion and posterior parietal callus. Protoconch partially visible, large, dark-brown. Outer lip thickened internally, with distinct external varix, thicker medially and thinner toward extremities, lacking distinct, flattened, beveled area in anterior direction; labial denticulation absent or reduced to very obscure undulations; varix groove distinctly excavated. Outer lip white, externally darkening to bright brownish-orange in varix groove adjacent to body whorl. Aperture wide, broader than lip thickness when measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally medium-brown with lilac stain at anterior end. Parietal wall convex with thin ventral callus wash that is thicker at anterior and posterior ends. Posterior callus in fully adult

shells forms peaked mound separated from posterior lip insertion by distinct gap. Left antero-ventral callus extends from anterior end of varix to level of third plication, producing sharp, distinct, and straight continuation of varix. Columella slightly concave, plications slender. First and second columellar plications completely separate, subequal in size. Third plication is subequal in size to first and second, fourth plication weaker and confined to aperture. Space between the plications increases in posterior direction, with fourth plication remote (i.e. distance between third and fourth plication distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally, ending in sharp points.

**Type material:** Holotype, MNRJ 7186 (length 34.7 mm, width 20.4 mm); Paratypes: ANSP 390361 (length 32.8 mm, width 19.3 mm); ANSP 399366 (length 27.7 mm, width 18.0 mm); ANSP 399995 (length 34.5 mm, width 20.4 mm); BM(NH) 1996071 (length 34.2 mm, width 20.9 mm); BMSM, 1006 (length 31.2 mm, width 19.8 mm); IBUFRJ 8463 Paratype 3 (length 37.2 mm, width 23.3 mm); IBUFRJ 8464 (length 32.0 mm, width 20.1 mm); MNHN. (length 30.7 mm, width 19.0 mm); MNRJ 7187 (length 28.1 mm, width 16.8 mm); MORG 33311 (length 33.4 mm, width 21.0 mm); MORG 33312 (length 27.0 mm, width 18.1 mm); MZUSP 28243 (length 31.6 mm, width 20.0 mm); USNM 880120 (length 25.2 mm, width 16.9 mm), all from off Vitória (20°20' S, 040°00' W), Espírito Santo State, Brazil, 60–70 m, trawled by shrimp fishing boats on muddy sand bottom; GAC M2861 (length 33.6 mm, width 19.9 mm), off Vitória, Espírito Santo State, Brazil, 50–70 m, trawled by shrimp fishing boats on silty sand; AMNH 213931 (length 29.9 mm, width 18.0 mm), off Espírito Santo State, Brazil, 50 m; AMNH 213930 (length 30.5 mm, width 18.2 mm); GAC M1426 (length 30.3 mm, width 18.7 mm), both from off northern coast of Rio de Janeiro State, Brazil, 50 m, muddy bottom.

**Type locality:** Off Vitória (20°20' S, 040°00' W), Espírito Santo State, Brazil, 60–70 m, trawled by shrimp fishing boats on muddy sand bottom.

**Geographic range:** From the northern coast of Rio de Janeiro State to the central coast of Espírito Santo State, Brazil (figure 13).

**Remarks:** In color pattern *B. analuciae* is most similar to *B. largillieri* and *B. guerrinii*, but they differ in shell shape, spire form (figures 6, 7, 8), ventral callusing, aperture width, shape and thickness of external lip, and columellar structure (figures 10, 11, 12).

*Bullata analuciae* is most similar, in shell shape and columellar structure, to *B. bullata*, but they differ in the color pattern, spire form, ventral callusing, and aperture shape and width.

*Bullata lilacina* and *B. matthewsi* differ in color pattern and geographical range.

**Etymology:** This species is dedicated to Ana Lucia

Rodrigues Peixoto who first collected most specimens aboard shrimp fishing boats.

*Bullata bullata* (Born, 1778)  
(Figure 3)

*Voluta bullata* Born, 1778: 205–206. Type information could not be directly obtained, holotype formerly in the Musei Caesarei Vindobonensis, Vienna, but declared missing (Tomlin, 1917: 225); type locality: Indian Ocean [in error, endemic to Bahia State, Brazil]; Born, 1780: 218; Tomlin, 1917: 255.

*Marginella bullata*.—d'Orbigny, 1841: 415; Sowerby, 1846: 401, pl. lxxvii, figs. 155, 159; Petit, 1851: 55; Reeve, 1860: 52; Reeve, 1864, pl. 1; Redfield, 1870: 225; Weinkauff, 1879: 24, pl. 4, figs. 3, 4; Paetel, 1885: 191; Smith, 1945: 71, fig. 950; Rogers, 1951: 89, pl. 24, fig. 5; Dance, 1976: 193, unnumbered figure.

*Voluta ovum* Gmelin, 1791: 3445.

*Marginella magna* Swainson, 1822: appendix: 12.

*Marginella (Volutella) bullata*.—Swainson, 1833; Adams and Adams, 1853: 192; Tryon, 1852: 35, pl. 10, figs. 3, 4; Fischer, 1883: 602; Tryon, 1883: 173, pl. 55, fig. 61.

*Marginella bellangeri* Kiener, 1834: 27–28, pl. 9, fig. 43; Catlow and Reeve, 1845: 291; Reeve, 1860: 52.

*Marginella cutieri* Deshayes, 1853: 75 (*Explication des Planches*); 1857–58: pl. 123, fig. 5; Redfield, 1870: 262.

*Bullata bullata*.—Jousseau, 1875: 250; Tomlin, 1917: 244; Coan, 1965: 189; Rios, 1970: 113, pl. 40; Oliveira *et al.*, 1972: 14; Rios, 1975: 117, pl. 35, fig. 506; Wagner and Abbott, 1975: 22003; Rios, 1985: 121, pl. 42, fig. 537; Covert, 1986a: 2; Covert, 1986b: 3; Covert and Lee, 1989: 4; Covert and Covert, 1990: 2, fig. 1; Rios, 1990: 5, fig.; Lipe, 1991: 2, pl. 1 fig. 10; Rios, 1994: 147, pl. 48, fig. 638; Bozzetti, 1994 p. 54; Covert and Covert, 1995: 92, fig. 66; Rosenberg, 1996, [gopher://erato.acnatsci.org:70/0R1815753-1816546-/wasp/text/waspgoph.cvt].

*Bullata cutieri* (Deshayes, 1853).—Jousseau, 1875: 251.

*Marginella (Volutella) bellangeri*.—Kobelt, 1878: 72, pl. 27, fig. 2.

*Marginella (Bullata) bullata*.—Thiele, 1929: 355, fig. 429; Eisenberg, 1981: 129, fig. 14.

*Closia (Bullata) bullata*—Wenz, 1943: 1376, fig. 3892.

*Marginella (Closia) bullata*—Morretes, 1949: 104.

*Marginella bullata*.—Santos, 1955: 113, unnumbered figure.

**Diagnosis:** Shell large (34–101 mm), slender; color pattern of numerous thin to very thin darker spiral bands crossed by thin axial lines on rosy-gray background; obsolete crenulation on outer lip; aperture wide, broader than lip thickness when measured ventrally; ventral callus reduced to obsolete wash.

**Description:** Shell large (34–101 mm), smooth, elongated, narrowly obovate (length:width ratio 1.51–1.96,  $\bar{x}$  = 1.83,  $s$  = 0.0946,  $n$  = 25), with about 5 whorls. Color pattern composed of numerous thin to very thin darker spiral bands crossed by thin, mostly pale or occasionally darker axial lines on rosy gray background (usually fading into pinkish-tan with time, in museum specimens). Axial lines are apparently associated with incremental growth lines. Spire immersed and covered by a vitreous callus, sometimes visible, rarely partly covered by lip insertion.



which imparts flattened to depressed shape to posterior end of shell. Protoconch darker than early teleoconch whorls, usually completely covered by vitreous callus. Outer lip thickened internally, with distinct external varix, thinner toward extremities, with an obscure, flattened, beveled area in anterior direction, and often abruptly thinned in anterior direction, labial denticulation usually reduced to obscure undulations, at most present as obsolete denticles. Varix groove generally filled forming wide, rounded, or flattened shelf. Outer lip white, externally darkening to orangish-brown, especially on varix groove adjacent to body whorl. Aperture wide, broader than lip thickness measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally brown, becoming white toward lip. Parietal wall convex with thin ventral callus wash. Posterior callus nearly obsolete. Left antero-ventral callus extends from anterior end of varix to level of third plication in gradual curve toward columella, resembling a fasciole. Columella slightly concave, plications slender to somewhat heavy. First and second columellar plications separate to fused distally, subequal in size. Third plication is subequal in size to first and second plications, with fourth plication subequal to slightly weaker and confined to aperture. Space between plications increases in posterior direction, with fourth plication remote (i.e., distance between third and fourth plication distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally.

**Material examined:** Types of *Marginella cucieri* Deshayes, 1853. MNHN unnumbered, Bahia, Brazil; IB-UFRJ 1540, off Salvador, Bahia State, Brazil, 5–10 m. B. Linhares col.; IBUFRJ 8471, off Salvador, Bahia State, Brazil, 5–10 m. B. Linhares col.; MZUSP 547, off Salvador, Bahia; MZUSP 15686, Mar Grande, Itaparica, Bahia State, Brazil, G. May, col.; MZUSP 27267, off Salvador, Bahia State, Brazil.

**Geographic range:** Endemic to Bahia State, Brazil (figure 13).

**Remarks:** *Bullata bullata* is most similar, in size and color pattern, to *B. matthewsi*, but they differ in background color, spire form, callus structure, aperture width, and labial denticulation. In addition, their geographical ranges are widely disjunct (figure 13).

See remarks under *B. guerrinii* and *B. analuciae*, and key for comparison with *B. bullata*.

*Bullata bullata* differs from *B. largillieri* and *B. lilacina* in size, shell shape, color pattern, structure of ventral callus, aperture width, and columellar structure.

Apparent spire, yellowish coloration and smaller size in original illustration of *Marginella cucieri* Deshayes, 1853 seemed to indicate that this species was a senior synonym of *B. matthewsi*. But in examining types, it became clear that they were smaller discolored *B. bullata*, two of them with atypically apparent spires (but covered with callus). The broad medial white band shown in the original illustration was due to shell deterioration. This

"variety" was later discussed by Sowerby (1846: 401, sp. 104; pl. 77, figure 159) who did not mention Deshayes's work.

*Bullata largillieri* (Kiener, 1841)  
(Figures 4, 9, 12)

*Marginella largillieri* Kiener, 1841: 43–44, pl. 11, fig. 3. Holotype not found, types were formerly deposited in Rouen Museum, but are now missing (P. Bonchet, personal communication, 1995). Type locality: Bahia, Brazil ("baie de Bahia" Kiener, 1841: 43, most probably Todos os Santos Bay); Catlow and Reeve, 1845: 292; Reeve, 1860: 52; Reeve, 1864, pl. VI fig. 22 a, b; Redfield, 1870: 240; Tomlin, 1917: 275; Dance, 1976: 195 unnumbered figure.

*Marginella largillieri*—Sowerby, 1846: 402, pl. lxxviii, figs. 175, 179, 180; Paetel, 1853: 31.

*Marginella largillieri*.—Petit, 1851: 52; Weinkauff, 1879: 44, pl. 5, figs. 2, 3; Rios and Oleiro, 1965: 17; Oliveira *et al.*, 1981: 271.

*Marginella (Volutella) largillieri*—Adams and Adams, 1853: 192; Kobelt, 1878: 72, pl. 27, fig. 9.

*Marginella ovum* Reeve, 1864: sp. 89, pl. XVIII, fig. 89a, b; Redfield, 1870: 247; Weinkauff, 1879: 65, pl. 12, figs. 6, 7; Paetel, 1855: 195.

*Marginella largillieri*.—Paetel, 1869: 35.

*Closia largillieri*.—Joussemaie, 1875: 255.

*Closia paros* Joussemaie, 1875: 255 (nomen novum for *Marginella ovum* Reeve, 1865); Tomlin, 1917: 257.

*Marginella (Closia) largillieri*.—Tryon, 1852: 47, pl. 12, figs. 77, 78.

*Marginella largillieri*—Paetel, 1855: 194.

*Marginella (Closia) largillieri*.—Morretes, 1949: 104.

*Closia largillieri*—Rios, 1970: 114, pl. 40; Rios, 1975: 117, pl. 35, fig. 508; Wagner and Abbott, 1975: 22008.

*Closia largillieri*—Oliveira *et al.*, 1972: 14.

*Persicula (Closia) largillieri*—Rios, 1985: 122, pl. 42, fig. 542.

*Persicula largillieri*.—Leal, 1990: 171, 399, 417.

*Marginella* sp. 65.—Lape, 1991: 2, pl. 1, fig. 12.

*Bullata largillieri*.—Lipe, 1991: 2, pl. 1, fig. 3; Rosenberg, 1996 [gopher://erato.acnatsci.org:70/0R1816346-1816945/.waspl/text/waspglyph.cvt].

*Closia largillieri*.—Bozzeti, 1992: 10.

*Bullata largillieri*—Rios, 1994: 147, pl. 45, fig. 639.

**Diagnosis:** Shell heavy, obovate to broadly obovate; color pattern of small, irregular cream spots arranged in axial rows, superimposed on light chocolate-brown background; spire completely immersed, covered by posterior labial insertion and posterior parietal callus; labial denticulation sharp and distinct; ventral callus heavy, continuous; aperture narrow; first and second plication distally fused, forming very strong plication ridge.

**Description:** Shell of medium size (14–29 mm in length), heavy, obovate to broadly obovate (length:width ratio 1.39–1.67,  $\bar{x}$  = 1.561,  $s$  = 0.0595,  $n$  = 25). Color pattern of small, irregular cream spots arranged in axial rows, on light chocolate-brown background, crossed by 1–3 indistinct darker spiral bands (1 near suture, 1 at mid-section of body whorl, and 1 near anterior end, this latter sometimes absent). Spotting somewhat to distinctly reduced on dark spiral bands. Spire completely im-

mersed, partially to completely covered by posterior labial insertion and posterior parietal callus. Protoconch not visible. Outer lip heavily thickened internally, with distinct, heavy external varix, thicker medially and thinner toward extremities, especially in posterior direction, with indistinct, flattened, beveled area in anterior direction, labial denticulation sharp and distinct, composed of approximately 24–36 denticles, varix groove excavated. Outer lip white, externally evenly colored a creamy brownish-orange, only very slightly darker in varix groove adjacent to body whorl. Aperture narrow, narrower than lip thickness measured ventrally. Aperture internally pale-brown. Parietal wall convex with continuous heavy ventral callus, thickening toward aperture, abruptly diminishing along collabral line just outside aperture, forming almost planar surface tangential to whorl. Callus extending to columella, next to distal ends of third and fourth plications. Posterior callus in fully adult shells forming rounded mound separated from posterior lip insertion by distinct gap. Left antero-ventral callus extending from anterior end of varix to level of fourth plication, with distinct furrow between second and third plications and producing a somewhat rounded continuation of varix. Columella concave, plications heavy. First plication much weaker than second, distally fused, effectively forming 1 very strong plication ridge, separated from parietal callus by distinct groove. Third plication is slightly stronger than fourth, both slightly emerging from aperture. Space between plications increases in posterior direction, fourth plication not remote. Third and fourth plications abruptly truncated and expanded distally, where they meet parietal callus.

**Material examined:** IBUFRJ S909, Rio do Fogo Beach, Rio Grande do Norte State, Brazil, L. Couto col.; MNRJ 5440, off Boipeba, Bahia State, Brazil; MNRJ HSL 4180, Barra Beach, Salvador, Bahia State, Brazil; PMC 939, off Salvador, Bahia State, Brazil, B. Linhares col.; GAC M2215, IBUFRJ 1469, off Itabapoana, Espírito Santo State, Brazil.

**Geographic range:** Rio Grande do Norte State to northern coast of Rio de Janeiro State, Brazil (figure 13).

**Remarks:** See remarks under *B. guerrinii*, *B. analuciae*, and *B. bullata*, and key for a comparison with *B. largillieri*.

*Bullata largillieri* is readily distinguished from *B. lilacina* and *B. matthewsi* by its distinctive color pattern, different columellar plications, and its more obovate shape.

A juvenile specimen examined (IBUFRJ 1469) shows second plication strongly angled toward and fused with the first, but plications are comparatively thin and sharp, and not yet heavily thickened. This juvenile shell has no external varix but it appears that it was just beginning to thicken the lip inside the aperture. Lip is thin, gradually beveled, and with a sharp edge, which is very narrowly opaque white externally. There is no trace of parietal callus.

*Marginella ovum* Reeve, 1865, renamed *Closia paros* Jousseaume, 1875, seems to represent *B. largillieri*, given mentions in the original description of its "curiously swollen" second columellar plication, immersed spire, narrow aperture, and denticulated lip.

*Bullata lilacina* (Sowerby, 1846)  
(Figure 5)

*Marginella lilacina* Sowerby, 1846: 402, pl. lxxviii, figs. 176–177. Holotype, BM(NH) 1880.9.15.2, type locality unknown; Petit, 1851: 55; Reeve, 1865, pl. xiv; Redfield, 1870: 240; Weinkauff, 1879: 46, pl. 4, figs. 3, 4; Paetel, 1888: 194; Matthews and Rios, 1967: 72; Kempf and Matthews, 1968: 93; Matthews and Kempf, 1970: 5; Matthews and Matthews, 1979: 71; Abbott and Dance, 1986: 234, unnumbered figure.

*Marginella (Volutella) lilacina*.—Adams and Adams, 1853: 192.

*Marginella (Closia) lilacina*.—Tryon, 1882: 47, pl. 12, fig. 80.

*Marginella (Volvarina) lilacina*.—Morretes, 1949: 105.

*Closia lilacina*.—Jousseaume, 1875: 255; Rios, 1970: 114, pl. 40; Rios, 1975: 118, pl. 35, fig. 509; Wagner and Abbott, 1978: 22008; Bozzetti, 1992: 10.

*Persicula lilacina*.—Oliveira *et al.*, 1981: 270.

*Persicula (Closia) lilacina*.—Rios, 1985: 121, pl. 42, fig. 538; Mello and Perrier, 1986: 133.

*Bullata lilacina*.—Lipe, 1991: 2, pl. 1, fig. 1; Rios, 1994: 147, pl. 45, fig. 640; Rosenberg, 1996. [gopher://erato.aenatsci.org:70/0R1816945-1817292-/wasp/text/waspgoph.cvt].

**Diagnosis:** Shell broadly obovate; color pattern of 2 pale-rose bands on rosy-brown background, outer lip white, externally pale- to dark-lilac; outer lip with distinct, flattened, beveled area in anterior direction, abruptly thinning in anterior direction forming siphonal "gutter"; first plication somewhat higher in ventral profile.

**Description:** Shell of medium size (19–33 mm in length), broadly obovate (length:width ratio 1.39–1.59,  $\bar{x}$  = 1.533,  $s$  = 0.0573,  $n$  = 25). Color pattern of 2 pale-rose medial spiral bands, and numerous, thin darker indistinct spiral lines, crossed by thin, mostly pale or occasionally darker axial lines on rosy-brown background. Spiral lines absent on medial spiral bands, usually fading in collection specimens. Axial lines apparently associated with incremental growth lines. Spire immersed, mostly covered by callus, partially covered by posterior lip insertion and posterior parietal callus. Protoconch completely covered to barely visible, dark. Outer lip heavily thickened internally, narrowing rather abruptly in anterior direction and in posterior direction, with distinct, flattened, beveled area in anterior direction; abrupt anterior thinning of lip effectively forming siphonal "gutter" (best seen in apical view). Labial denticulation distinct, fine to coarse, composed of approximately 20 denticles. Varix distinct, heavy, varix groove deeply excavated. Outer lip white, externally pale- to dark-lilac, orangish-brown in varix groove adjacent to body whorl. Aperture narrow to moderately narrow, narrower than lip thickness when measured ventrally, broadest at level of plications, narrowing in anterior direction. Aperture



internally lilac with lilac stain at anterior end. Parietal wall convex with continuous, moderately heavy ventral callus, thickening toward aperture, thinning along indistinct collabral line just outside aperture, reaching fourth plication, usually indistinctly transversely undulated, extending to columella as a wash. Posterior callus in fully adult shells forming very low, rounded mound barely separated from posterior lip insertion by indistinct gap. Left antero-ventral callus extending from anterior end of varix to level of third plication as heavy wash, somewhat resembling indistinct fasciole, with lilac coloration, and slight furrow between second and third plications. Columella slightly concave, plications heavy. First and second columellar plications completely separate, subequal in size, and slightly stronger than third and fourth, first somewhat higher in ventral profile (best seen in lateral view). Third plication is subequal in size to fourth, both slightly emerging from aperture. Space between plications increasing in posterior direction, with fourth plication not remote. Third and fourth plications truncated and slightly expanded distally.

**Material examined:** AMNH 194277, off Fortaleza, Ceará State, Brazil; MNRJ 4175, Poço Beach, Paraíba State, Brazil; MNRJ HSL 4176, Camocim, Ceará State, Brazil; PMC 476, off Fortaleza, Ceará State, Brazil; IBUFRJ S924, off Rio do Fogo, Rio Grande do Norte State, Brazil, 5–6 m, 04/1997; MZUSP 16339, off Fortaleza, Ceará State, Brazil; MZUSP 29716, off Fortaleza, Ceará State, P. Montouchet col., *ex-pisce Amphichthys cryptocentrus* (Valenciennes, 1837).

**Geographic range:** Amapá State to Ceará State, Atol das Rocas, Brazil (figure 13).

**Remarks:** Although *B. lilacina* has been reported from coast of Bahia (Rios, 1994), all specimens collected in Bahia that we observed, were in fact bleached *B. largillierii*, a species easily recognizable by its columellar structure.

The color pattern of *B. lilacina* in most preserved shells seems to consist of only 2 wide whitish bands. The examination fresh-collected shells (IBUFRJ S924) revealed thin and numerous spiral and axial lines, which apparently fade with passing of time.

*Bullata lilacina* differs from *B. matthewsi* in the spire form, and structure of parietal callus and columella. For comparison with other species, see previous remarks and key.

*Bullata matthewsi* (van Mol and Tursch, 1967)  
(Figure 6)

*Marginella (Prunum) matthewsi* van Mol and Tursch, 1967: 196–197, fig. 1, holotype; Stanford University Paleo-Type Collection 9856, type locality: off Fortaleza, Ceará State, Brazil, 36 m, *ex-pisce Amphichthys cryptocentrus* (Valenciennes, 1837).

*Marginella matthewsi*.—Matthews and Rios, 1967: 72; Kempf and Matthews, 1968: 93; Matthews, 1968: 248; Abbott and

Dance, 1986: 235 (unnumbered figure; Matthews and Matthews, 1979: 71)

*Prunum matthewsi*—Wagner and Abbott, 1975: 22009

*Bullata matthewsi*.—Rios, 1970: 113, pl. 40; Rios, 1975: 117, pl. 35, fig. 507; Rios, 1985: 121, pl. 12, fig. 535; Rios, 1990: 9, unnumbered figure; Lipe, 1991: 2, pl. 1 fig. 4; Bozzetti, 1994: 54, fig. 1; Rios, 1994: 147, pl. 48, fig. 635; Rosenberg, 1996, [gopher://erato.acnatsci.org:70/0R1S17292-1S171966/.wasp/.text/waspgopl.txt].

**Diagnosis:** Shell moderately large; color pattern of numerous thin to very thin tawny- to brownish-orange spiral bands crossed by numerous axial lines on pale-orange background; spire slightly but distinctly apparent; outer lip in anterior direction with very distinct, flattened, broadened, beveled area and distinct anterior trough or siphonal “gutter”; parietal wall with continuous, thin but distinct, ventral callus; first columellar plication distinctly larger and thicker than other 3.

**Description:** Shell moderately large (39–53 mm in length), obovate (length:width ratio 1.65–1.71,  $\bar{x}$  = 1.681,  $s$  = 0.0211,  $n$  = 7), with 4.5–5 whorls. Color pattern of numerous thin to very thin tawny- to brownish-orange spiral bands crossed by thin, mostly pale or occasionally darker axial lines on pale-orange background. Two medial spiral bands of less dense coloration present. Axial lines apparently associated with incremental growth lines. Spire distinctly apparent, extremely low; dome-like, partially covered by posterior lip insertion and to a limited extent by posterior parietal callus. Protoconch mamillated, completely visible. Outer lip thickened internally, with distinct external varix, rather abruptly narrowed in posterior direction, with very distinct, flattened, broadened, beveled area in anterior direction; abruptly thinning in anterior direction, effectively forming a distinct trough or siphonal “gutter” (best seen in apical view), labial denticulation indistinct to distinct, fine to coarse, composed of approximately 27–30 denticles; varix groove distinctly excavated. Outer lip white, externally pale orange-cream, darkening to a pale brownish-orange in varix groove adjacent to body whorl. Aperture wide, broader than lip thickness measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally nearly white, darker banding showing through very faintly. Parietal wall convex, with thin, but distinct and continuous ventral callus, forming very indistinct collabral ridge just inside aperture, extending to columella as a wash. Second indistinct collabral callus ridge present further inside aperture and abruptly ending just posterior to fourth plication, leaving distinct gap between them. Profile of collabral ridge even with the tops of the plications. Posterior callus in fully adult shells forming indistinct, low, rounded mound barely separated from posterior lip insertion by indistinct gap, and continuing in short arc toward aperture. Left antero-ventral callus extending from anterior end of varix to level of third plication as heavy deposit somewhat resembling indistinct fasciole, with somewhat distinct furrow between second and third plications. Columella nearly straight, plications strong. First columellar plica-

tion distinctly larger and thicker than other three, distinctly raised in ventral profile (best seen in lateral view), broadened, flattened, and abruptly merging with anterior edge. First and second columellar plications completely separate. Posterior three plications subequal in size, all emerging from aperture to progressively greater extent in anterior direction. Space between plications subequal, with fourth plication not remote. Posterior three plications gradually narrowing distally.

**Material examined:** Paratype, AMNH 134492, off Mucuripe, Ceará State, Brazil; PMC 939, off Fortaleza, Ceará State, Brazil; IBUFRJ 8925, off Fortaleza, Ceará State, Brazil; GAC M1325, off Fortaleza, Ceará State, Brazil; GAC M2704, off Fortaleza, Ceará State, Brazil; MZUSP 27308, off Fortaleza, Ceará State.

**Geographic range:** Maranhão State to Rio Grande do Norte State, and Fernando de Noronha Island (figure 13).

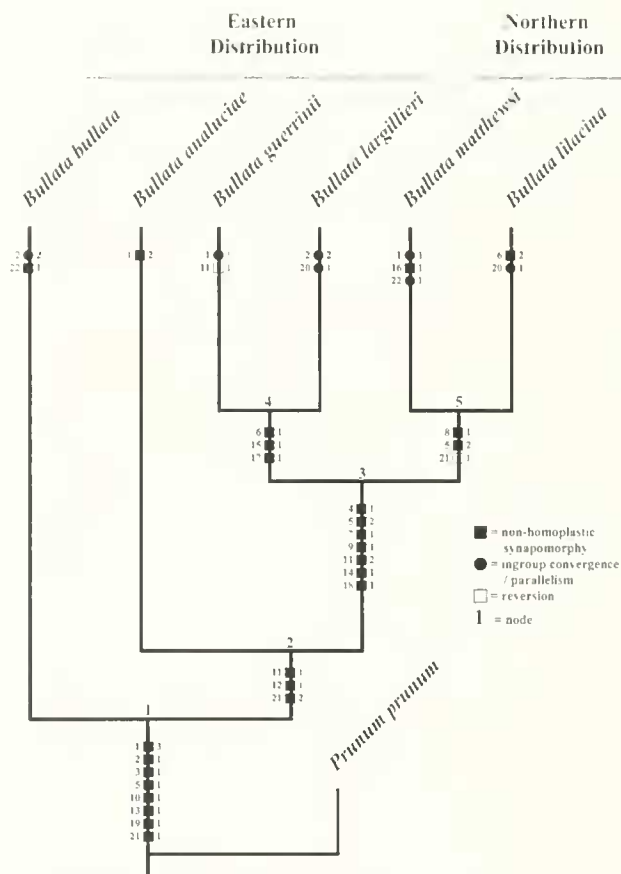
**Remarks:** *Bullata matthewsi* has a distinctly apparent spire, similar to that of *B. guerrinii* but they differ in spire height, color pattern, color patten. For comparison with congeneric species see specific remarks above and dichotomic key.

## PHYLOGENY AND BIOGEOGRAPHY

Preliminary results of a cladistic analysis of the genus *Bullata*, using conchological characters, are reported; further analysis using anatomical data is intended and will be published at the earliest opportunity.

In this analysis, 22 conchological characters with a total of 53 states were used (Appendix). Character polarization was done through outgroup comparison method (Maddison *et al.*, 1984). The type species of *Prunum* Herrmannsen, 1850 [*P. prunum* (Gmelin, 1791)] was selected since this genus was proposed as the sister group to *Bullata* by Covert and Covert (1995: 92). The cladogram was calculated using Tree Gardener 2.2 software (Ramos, 1998) which is basically a graphic interface for Hennig86 (Farris, 1988).

A single most parsimonious tree (figure 14) was obtained (length = 37, CI = 81, RI = 69). The monophyly of *Bullata* (node 1) is sustained by 7 synapomorphies. Node 2, containing all species *Bullata* except *B. bullata*, is sustained by 2 synapomorphies (presence of posterior callus mound, partially thickened ventral callus, spotted color pattern). Node 3 is sustained by 6 synapomorphies (very thick external lip, distinct labial denticulation, beveled area on external lip, narrow aperture, furrow on anterior callus, fourth plication not remote). Node 3 gives origin to 2 branches, one with *B. matthewsi* and *B. lilacina* as terminal species, the other with *B. largillieri* and *B. guerrinii*. Node 4 is defined by the presence of siphonal gutter, ventral callus completely thickened, larger first plication, and reversion of color pattern to white spots on a brown background. Node 5 is sustained by the labial coloration that extends beyond the varix



**Figure 14.** Single most parsimonious phylogenetic tree obtained from cladistic analysis of species of *Bullata* based on shell characters. *Prunum prunum* (Marginellidae) is the outgroup. See Appendix 1.

groove, small first plication and an enlarged second plication fused with first one.

Our feeling before the analyses was that *B. bullata* and *B. matthewsi* would group as sister taxa, due to similarities in size and color pattern. But the several synapomorphies of nodes 2, 3, and 5, not shared by *B. bullata*, grouped *B. matthewsi* as sister species of *B. lilacina*.

The character optimization used in colour pattern (21) is only one of two equally parsimonious interpretations. Another possibility would be that the spotted pattern appeared as a parallelism between *B. analuciae* and node 4.

Covert (1986c) proposed that the direct mode of development within a benthic egg capsule present in the Marginellidae would greatly reduce the dispersal abilities of its species, confining the distribution of species to a single zoogeographic province and many with even narrower distributions within these provinces. Scheltens (1989) found that there is significant relationship between the lack of planktonic larvae and distribution range. The distribution of the species of *Bullata* confirms these statements, with the very narrow distribution ranges of *B. bullata*, *B. analuciae*, and *B. guerrinii* and the relatively wider, but still confined to parts of the Brazilian coast, distributions of *B. largillieri*, *B. lilacina*, and

*B. matthewsi*. However, some capabilities for non-larval dispersal might be present, most probably by rafting of egg capsules and juveniles (Scheltema, 1989; Leal and Bouchet, 1991), since these three last species were able to colonize, respectively the Vitória Seamount (Leal, 1990), and Atol das Rocas and Fernando de Noronha Archipelago (Matthews and Kempf, 1970). All of these localities are separated from the continental shelf by depths greater than 2000 m, with Atol das Rocas and Fernando de Noronha, separated by distances greater than 300 km.

The geographic distribution of the genus along the Brazilian coast (figure 13) suggests two major patterns of distribution, with a slight overlap due to the extensive ranges of *B. largillieri* and *B. lilacina*: a northern species group, comprising *B. matthewsi* and *B. lilacina*; and a eastern species group, comprising *B. bullata*, *B. analuciac*, *B. largillieri* and *B. guerrinii*. The resulting cladogram is congruent, to a certain extent, with these geographic groups. The northern group corresponds to node 5. The eastern group is paraphyletic and consists of node 4 plus *B. analuciac* and *B. bullata*.

These patterns appear to follow two major oceanographic current patterns present along the Brazilian coast: the northern group, associated with the Guyana current and the eastern group, associated with the Brazil current. It is possible that the divergent currents along with intracapsular mode of development may have contributed to isolate northern and eastern populations, facilitating speciation events.

Key to species of *Bullata*:

- 1a. Shell with distinct cream spots on caramel- or dark-brown background and with faint spiral banding ..... 2
- 1b. Shell lacking cream spots, color pattern of few to many bands ..... 4
- 2a. First and second columellar plications completely separate, subequal in size; parietal callus restricted to posterior end, not forming collabral ridge; aperture much broader than lip thickness; fourth plication remote (i.e. distance between third and fourth plication distinctly greater than distance between second and third); lip lacking denticulation, moderately thickened ..... *Bullata analuciac* new species
- 2b. Second columellar plication greatly enlarged, fused with first; parietal callus moderate to heavy, forming weak to distinct collabral ridge; fourth plication not remote ..... 3
- 3a. Spire completely immersed, usually covered by posterior labial insertion; aperture narrower than lip thickness, only slightly broader in anterior direction; parietal and other ventral callus white or nearly so; lip greatly thickened; third and fourth plications distinctly truncate and expanded at distal ends ..... *Bullata largillieri* (Kiener, 1841)
- 3b. Spire not immersed, slightly apparent, proto-

- conch exposed; aperture as broad or broader than lip thickness medially, distinctively broader in anterior direction; parietal and other ventral callusing brown-tinged; lip moderately thickened; third and fourth plications gradually narrowing distally, ..... *Bullata guerrinii* new species
- 4a. Shell smaller, 19–33 mm in length; color rosy-brown with 2 distinct light pink, broad bands; lip strongly denticulate; aperture narrower than lip thickness; third and fourth plications distinctly truncate at distal ends; lip strongly denticulate, greatly thickened; color pattern of 1 or 2 broad spiral color bands ..... *Bullata lilacina* (Sowerby, 1846)
- 4b. Shell larger, 34–98 mm in length; color grayish-to orange-brown, without distinct broad spiral bands, with numerous distinct thin lines of varying thickness; lip at most weakly denticulate; aperture much broader than lip thickness; third and fourth plications gradually narrowing distally, ending in sharp points; color pattern of numerous, small spiral bands ..... 5
- 5a. Lip weakly crenulated, with a flattened, broadened area in anterior direction, forming a weak siphonal "gutter"; spire slightly but distinctly apparent; first plication much stronger than other plications and distinctly higher in profile; fourth plication not remote, distance between third and fourth at most only slightly greater than distance between second and third ..... *Bullata matthewsi* (van Mol and Tursch, 1967)
- 5b. Lip at most faintly crenulated, lacking flattened area in anterior direction; anterior 2 columellar plications subequal in size; spire immersed, apex flattened to depressed, usually covered; first plication as strong as or weaker than other plications, not higher in profile; fourth plication remote ..... *Bullata bullata* (Born, 1778)

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**Appendix 1.** Character list and table.

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Character 1: Spire shape, nonadditive, 4 steps, CI = 75, RI = 0

[0]—Apparent, conic, very low; [1]—Apparent dome-like; [2]—Involute flat; [3]—Involute, sunk.

Character 2: Posterior labial insertion, nonadditive, 3 steps, CI = 66, RI = 0

[0]—on body whorl; [1]—posterior to body whorl; [2]—covering apex.

Character 3: Varix, nonadditive, 1 step, CI = 100, RI = 100

[0]—narrow; [1]—wide.

Character 4: Lip thickness, 1 step, CI = 100, RI = 100

[0]—thick; [1]—very thick;

Character 5: Labial denticulation, nonadditive, 2 steps, CI = 100, RI = 100

[0]—absent; [1]—crenulated; [2]—distinct;

Character 6: Labial coloration, nonadditive, 2 steps, CI = 100, RI = 100

[0]—restrict to varix groove; [1]—extending ventrally; [2]—3 colors;

Character 7: Anterior beveled area on external lip, 1 step, CI = 100, RI = 100

[0]—absent; [1]—present;

Character 8: Siphonal gutter, 1 step, CI = 100, RI = 100

[0]—absent; [1]—present;

Character 9: Aperture width, 1 step, CI = 100, RI = 100

[0]—wide; [1]—narrow;

Character 10: Ventral callus, 1 step, CI = 100, RI = 100

[0]—absent; [1]—present very sinuous;

Character 11: Callus thickness, additive, 3 steps, CI = 66, RI = 0

[0]—thin; [1]—thick locally; [2]—thick all over;

Character 12: Posterior callus mound, 1 step, CI = 100, RI = 100

[0]—absent; [1]—present;

Character 13: Anterior callus, 1 step, CI = 100, RI = 100

[0]—simple; [1]—fasciole like;

Character 14: Furrow on anterior callus between second and third plications, 1 step, CI = 100, RI = 100

[0]—absent; [1]—present;

Character 15: first plication size, nonadditive, 2 steps, CI = 100, RI = 100

[0]—subequal; [1]—small; [2]—large;

Character 16: first plication in ventral profile, 1 step, CI = 100, RI = 100

[0]—normal; [1]—raised;

Character 17: second plication, 1 step, CI = 100, RI = 100

[0]—subequal; [1]—larger fused with first;

Character 18: fourth plication, 1 step, CI = 100, RI = 100

[0]—remote; [1]—not remote;

Character 19: False fifth plication, 1 step, CI = 100, RI = 100

[0]—present; [1]—absent;

Character 20: Shape of distal end of plications, 2 steps, CI = 50, RI = 0

[0]—thin evenly; [1]—trimate;

Character 21: Color pattern, nonadditive, 4 steps, CI = 50, RI = 0

[0]—few wide bands; [1]—many thin wide bands crossed by axial lines; [2]—spotted on wide bands;

Character 22: Size, 2 steps, CI = 50, RI = 100.

[0]—small to medium; [1]—large;

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